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THE DEVELOPMENT AND RELATIONSHIP OF MONOCLEA.[1]

CONTRIBUTIONS FROM THE BOTANICAL LABORATORY OF
THE JOHNS HOPKINS UNIVERSITY, No. 2.

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(WITH PLATES XVI AND XVII)

While studying and collecting the native Piperaceae of Jamaica, in the spring of 1903, I also preserved plants in various stages of development of the liverwort *Monoclea Forsteri* Hook. The results of the study of the material of this little known form are given in the following pages.

Monoclea occurs in Jamaica chiefly on wet rocks and banks in the mountain forests (Campbell '98). The most luxuriant growth of it seen by the writer was one of many meters in extent in a small depression near New Haven Gap in the Blue Mountains. This depression was filled up considerably by living and decaying vegetation, but the water in it stood at such a level that the tangles of Monoclea and associated plants were practically floating upon its surface. The appearance of a mat of Monoclea is not so much like one of the more attenuated plants of Marchantia or Fegatella as it is like a mat of gigantic Pellia, though the edges of the thallus are often more crisped or curled upward than in the latter genus. The plants growing in the water at New Haven Gap were often 3^{cm} wide, in the case of the broader branches, while elsewhere they seldom exceeded 2^{cm}. The growing ends of these aquatic plants were almost erect, apparently because of the wet substratum, since this peculiarity did not seem to be attributable to the direction from which light reached them.

A majority of the plants found were sterile, and in the case of the plants growing in wetter situations fertile plants were very scarce. In groups of plants growing in the damp ravines, where the substratum was not so completely saturated with water, though the air was saturated with water vapor, fertile plants of both sexes were easily found.

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The older female plants were most readily distinguishable by the presence of the large tubular involucre enclosing the large sporogonia. Male plants were readily found, being slightly smaller than the female plants, but in most of them the antheridia had matured and discharged, and only the shriveled male receptacle remained. Careful sorting of large amounts of material was necessary at the season I was in Jamaica, in order to discover young male receptacles with developing antheridia in them.

<div align="center">HISTORICAL RÉSUMÉ.</div>

Monoclea Forsteri was originally described by HOOKER ('20), from material collected (in "Insulae Australes") by FORSTER while accompanying Captain COOK on his famous voyage. HOOKER was aided also by a drawing and a manuscript description of the plant by FORSTER, who had named it *Anthoceros univalvis*. The general form of the non-costate thallus, the simple involucre, the lack of a female receptacle, and the structure of the open capsule, all features which were shown in HOOKER's *fig. 1.* were apparently taken from FORSTER's drawing. By study of the specimens HOOKER made out that the unopened capsule was cylindrical, and that it opened by a single lateral slit. He also figured the spores and elaters and noted the presence of three well-developed capsules in a single involucre, each with its own tubular calyptra.

The removal of the plant from the genus Anthoceros, and the establishment of the genus Monoclea to receive it, was based by HOOKER on the absence of the columella and the presence of but one valve in the open capsule.

Ten years later HOOKER ('30) described as *Monoclea crispata* a liverwort found in the island of St. Vincent, in which he found a univalve capsule like that of Monoclea, and a columella like that of Anthoceros. This latter led him to think that he had probably overlooked a columella in *M. Forsteri,* and to decide that Monoclea was probably intermediate between Anthoceros and the Jungermanniaceae.

TAYLOR ('44, '45), apparently after consulting HOOKER's later paper only, added two other species to the genus Monoclea.

A year later NEES VON ESENBECK ('46) established the genus Dendroceros to contain HOOKER's *M. crispata* and Taylor's species,

but failed to recognize the full importance of the differences between the involucre, calyptra, and sporogonium of *M. crispata* and those of the other forms included in the genus by HOOKER and TAYLOR, and apparently based the division of the genus chiefly on the columella.

GOTTSCHE ('58) studied material of Monoclea from Chili. From this he described the gross and minute structure of the vegetative thallus, noting the presence of two types of (non-tuberculate) rhizoids and the occurrence of fungus hyphae in certain cells of the thallus. The involucre he thought completely closed at first. He also described the structure of the mature sporogonium, from the foot to the capsule, with its one-layered wall, unicellular elaters, and roughened spores. On the basis of these observations GOTTSCHE clearly distinguishes *M. Forsteri* from the species of Dendroceros with which it had been associated by HOOKER, TAYLOR, and NEES, and seems to find in it close resemblances to Pellia and Blasia, with which he frequently compares it. He also remarks on the outward likeness to Marchantia which had been noted earlier by HOOKER ('20, p. 176).

Nine years later still GOTTSCHE ('67) discovered the elevated, oval male receptacle on plants of Monoclea from Mexico.

The next important worker on the genus was LEITGEB ('77), who confirmed the work of Gottsche on the structure of the thallus, calyptra and capsule, and insisted on the similarity in structure and branching of the thallus with that of Pellia and Symphyogyna, rather than with that of the dichotomous, areolate Marchantiaceae. He described the slender, thick-walled rhizoids, found by GOTTSCHE ('58), as generally distributed over the under side of the thallus, and as lying parallel to it, while the larger, thin-walled ones are, as GOTTSCHE showed, confined to the median portion of the thallus and stand out perpendicular to the latter. LEITGEB found that the involucre arises as a depression in the tip of the thallus, being closely like that of Pellia in origin and structure. He also discovered that the involucre is independent in its development of that of the sporogonium, and even of fertilization. No young archegonia or embryos were found. The mature archegonia occur in groups of eight or ten, have a large venter, and a long twisted neck. The capsule he thinks imperfectly four-valved. From these facts LEITGEB concludes that Monoclea is more closely related to Pellia than to any of the Marchantiaceae.

In 1881 LEITGEB studied alcoholic material of male and female plants of a Monoclea from New Zealand, the male plants of which had earlier been described as *Dumortiera dilatata*, and found that, except in the larger size of the plants and of the involucre, they agreed closely with *Monoclea Forsteri*. In the male plants he found that the form and distribution of the male receptacles was as described by GOTTSCHE ('67). The receptacles he likens to those of Fegatella, and notes that the elongated, conical antheridia are secondarily sunken in the cavities of the receptacle. These characters of the male plant he thinks show as striking a resemblance to the Marchantiaceae as do those of the female plant to the Jungermanniaceae, but which set of characters is to preponderate as an index of relationship LEITGEB does not definitely decide.

SCHIFFNER('93), in characterizing the genus Monoclea, apparently overlooks the later papers of both GOTTSCHE and LEITGEB, and states that the male plant is unknown. He also says that the wall of the capsule is of two layers of cells, though both GOTTSCHE and LEITGEB say it is one-layered. SCHIFFNER is then naturally led to follow LEITGEB's earlier conclusion ('77) that Monoclea is shown by the female plant and sporogonium to be closely related to Pellia.

Coincidently with SCHIFFNER's work appeared a paper by RUGE ('93), in which he described the development of the male receptacle and the antheridium, as worked out on preserved material from Venezuela, more completely than had been done by LEITGEB. According to RUGE several transverse walls appear in the primarily superficial antheridium mother-cell before any longitudinal ones are formed. The series of figures given does not show the details of the further development of the antheridium clearly, and the series for the archegonium is still less satisfactory.

In this description of the female plant RUGE agrees with GOTTSCHE and LEITGEB, but gives more details as to the development of the archegonial cavity. RUGE, for some reason not clear to the writer, described the slender rhizoids as being also thin-walled and the larger ones as thick-walled, the exact contrary of the condition found by GOTTSCHE, LEITGEB, and the present writer.

CAMPBELL ('98) in a short paper reviews briefly the bearing of the work of HOOKER, GOTTSCHE, LEITGEB, and RUGE, and points out

that the work of the latter (though Ruge apparently failed to appreciate this) materially adds to the likenesses between Monoclea and the Marchantiaceae, which Leitgeb ('81) had already noted.

From the presence of two types of rhizoids, the development of the male receptacle and the antheridium, and from the structure of the mature archegonium made out by Campbell himself, he concludes that Monoclea is to be included in the Marchantiaceae. The absence of ventral scales and of the air chambers, characteristic of the Marchantiaceae, he thinks cannot be considered a greater objection here than in the case of Dumortiera, in certain species of which he has shown that the air chambers are not present at any stage of development.

THE MALE RECEPTACLE.

The male receptacle of Monoclea is a slightly elevated oval area, $4-10^{mm}$ long and $2-3^{mm}$ broad, on the median line of the upper surface of the thallus (*fig. 1*). In general appearance it is something like the male receptacle of Fegatella, but in origin it resembles more closely that of Fimbriaria (Campbell '95), since the receptacle is not sunken into the thallus and is not the product of several growing points, both of which features Cavers ('04) has shown to be characteristic of Fegatella.

The antheridia of Monoclea occur in groups of fifteen to fifty, arranged in four to six rather indefinite longitudinal rows along the receptacle (*figs. 1, 2, 4, 6*). They arise in acropetal succession, and the antheridia of the same receptacle may range in development from those of a few cells each at the anterior end to nearly ripe antheridia at the posterior end (*figs. 8, 9*).

The male receptacle arises by the upward growth of the cells of the thallus round about and among the antheridia of a group (*figs. 6, 9*). This upward growth of the sterile cells is subsequent to the formation of the antheridium rudiments (*fig. 6*), and thus progresses, like the development of the latter, from behind toward the growing point. When the formation of antheridia ceases for a time, the growing point which has given rise to the antheridia pushes on, forming a stretch of vegetative thallus of normal thickness (*fig. 9*). Thus the receptacle has an abrupt ending in front, with an elevated and slightly overhanging margin, like that on the lateral and posterior edges (*figs. 2, 3, 8, 9*).

Three or four successive series of receptacles may often be seen on the same plant (*figs. 1, 3*). The youngest of these appear as crescentic regions at the growing point, with only the posterior edge slightly elevated above the thallus (*figs. 1, 4*). Whether more than one series of receptacles arise in one year was not made out with certainty, but I am inclined to believe that one series may be formed in each of the two rainy seasons that occur in Jamaica each year. Not infrequently a receptacle is found which extends up each branch from the point of forking of the thallus. This is due to the division of the growing point into two after the formation of antheridia has begun. The series of antheridia from the two growing points are clearly distinguishable in the young receptacle (*fig. 5*).

The older receptacles, after the ripening and discharge of their antheridia, become somewhat shriveled and brown, but finally disappear only with the progressive decay of the plant from the base (*figs. 1, 3*).

THE ANTHERIDIUM.

The mother-cell of the antheridium is first distinguishable when it is but a few cells back from the initial of the thallus, but the exact age or portion of the segment from which it arises was not determined. It is first recognizable because of its greater size and the darker staining of its contents, by its failure to divide by perclinal walls as early as the surrounding cells, and finally by the gradual separation of its lateral walls from those of the surrounding cells (*fig. 6*). This separation of the lateral cell-walls begins at the outer surface, and even before it is completed the surrounding cells begin to push upward more rapidly than the antheridium itself, and soon close in above it to a narrow pore (*figs. 6, 8, 9, 13*). Thus each antheridium finally comes to lie in a long-necked, flask-like cavity in the male receptacle. From the cells lining this cavity, club-shaped unicellular hairs are formed, which probably secrete the abundant slime that completely fills the older cavities around the antheridium and oozes out at the neck of the cavity (*figs. 8, 9, 13*). In paraffin sections this slime, with the imbedded hairs, has the appearance of a shrunken cellular jacket. The similar mass of slime in the archegonial cavity led GOTTSCHE ('58, *fig. 16*) to describe this mass as a structureless membrane, bearing hairs.

Soon after the separation of the antheridium mother-cell from the surrounding cells, it divides transversely into a terminal or body cell and a basal or stalk cell. The latter remains attached to the cells at the bottom of the pit, while the former is free from all but the stalk cell (*figs. 6, 10, 13*). The body cell soon becomes remarkable because of its denser contents and its more active division. It first divides twice transversely, and thus gives rise to four primary cells in the body of the antheridium (*figs. 6, 10*). Meantime the stalk cell of the antheridium divides into two, the upper one of which usually remains undivided for some time, while the lower one soon divides by a transverse wall (*figs. 11, 12, 13*). There are thus usually seven tiers of cells in the antheridium at this stage. Of these the three basal ones are concerned with the formation of the stalk, while the four terminal ones give rise to the body of the antheridium (*figs. 11, 12, 13*).

The stalk is more evident in the younger antheridium, since in the older ones, though it is several cells broad, it is usually crushed down by the rapid elongation of the antheridium, which pushes upward against the roof of the antheridial cavity and downward upon the stalk (*figs. 9, 13*).

The first longitudinal wall in each of the four cells of the body of the antheridium is a diametric one (*fig. 15*). Each of the two cells so formed is then cut by a radial, longitudinal anticline, and thus quadrants are formed (*fig. 16*). The next wall appearing in each quadrant is a pericline, which cuts off an outer wall cell from an inner spermatogenous one (*figs. 11, 13, 17*). Next there appears in each wall cell a radial anticline (*fig. 17*), and this is soon followed by other longitudinal and some transverse anticlines, but no periclines are formed in the wall cells except at the tip of the antheridium. Here the cells of a small group divide by one or two periclines, and thus give rise to the thickened terminal area in the wall of the mature antheridium (*figs. 9, 14*). The rest of the wall of the mature antheridium is one-layered throughout. The cells of the wall at maturity are somewhat elongated longitudinally to the antheridium and are about equally thickened on all sides. The place and mechanism of the opening of the antheridium were not observed.

The primary spermatogenous cell of each quadrant of the antheridium breaks up, at first in a pretty regular manner, by approximately

longitudinal anticlines (*figs. 18, 19, 20*).   Then by the appearance
of other longitudinal and transverse anticlines a very large number
of spermatogenous cells are formed.   The nuclear divisions in these
spermatogenous cells occur simultaneously over larger or smaller
blocks, commonly extending over one-tenth to one-fifth the area of
a longitudinal section of the antheridium, but never over the whole
of it at once.   In several of the antheridia examined there were found
to be from 35 to 50 of these cubical spermatogenous cells on a single
diameter, and from 125 to 160 of them in the length of the antheridium.
This means that there are from 100,000 to 250,000 of these cells in a
well-developed antheridium.   Each of these cubical cells divides
later by a diagonal wall to form two triangular-prismatic sperma-
tozoid mother-cells.   There are thus formed from 200,000 to 500,000
spermatozoids in each antheridium.

The organization of the spermatozoid in the mother-cell begins,
as in other described liverworts, by the elongation and coiling of the
nucleus.   The presence of a blepharoplast was not demonstrated.
When mature the spermatozoid is coiled to about one and a half turns
in a flat spiral, whose axis is perpendicular to the broader side of the
triangular-prismatic mother-cell.

The most striking peculiarity shown in the development of the
spermatozoid is the fact that the individuality of the chromosomes
is visibly persistent in the ripe spermatozoid.   Careful study of the
mitotic figures in spermatogenous cells at various stages of develop-
ment showed the number of chromosomes to be eight or ten.   In
preparations of ripe antheridia, which had been fixed in Flemming's
solution and stained in Flemming's triple stain, when washed so as to
show well the chromatin in the vegetative nuclei round about, the
spermatozoids appeared as single dark blue coils.   When however
the sections were washed out more completely, so that even the nuclei
were of a faint blue, the color remaining in the spermatozoid was con-
fined to a number of fine threads of nearly the length of the sperma-
tozoid.   These threads were twisted about each other slightly so that
each thread in its length made a complete turn about the nearly
cylindrical spermatozoid (*fig. 8a*).   A careful count of these threads,
which could best be made in optical transverse sections of the coils
of the spermatozoid, showed that the number is constant and identical

with that of the chromosomes in the spermatogenous cells (*fig. 8b*). The fact that no other part of the spermatozoid retained the stain, and the constant agreement in number just mentioned, seems to leave no doubt that these threads in the spermatozoid are the greatly elongated chromosomes. The significance of this unique individuality of the chromosomes in the nearly ripe spermatozoid might be discovered by a study of the process of fertilization and the behavior of these chromosomes in the fusion nucleus of the fertilized egg. This I was unable to accomplish because of a lack of material of the particular stage needed.

THE ARCHEGONIUM.

The portion of the thallus from which the archegonia develop is not as much differentiated from the vegetative part as is the male receptacle. The archegonia arise in acropetal succession, in groups of six to ten, on the upper surface of the thallus just back of the growing point. At about the time of origin of the first archegonia of a group, for these differ considerably in age, the thallus begins to thicken just behind the growing point. A longitudinal section of this region at this time would look much like that of a young male receptacle (*figs. 26, 27*). Soon the upper anterior edge of this thickening grows forward to form a hood-like involucre above the archegonia (*fig. 28*). This hood-like roof above the archegonia keeps pace with the advance of the growing point below, and thus is formed the long, tubular involucre, which may become 15^{mm} or more in length, though seldom more than $3-4^{mm}$ in width (*figs. 22, 29, 30, 31*). Though widely open at first the involucre is finally closed anteriorly except for a very narrow slit, the edges of which fit together closely (*figs. 22, 29, 31*). After a growing point has given rise to a single series of archegonia and has done its part in forming the lower side of the involucre its activity ceases. Then a new growing point appears on each side of the involucre at the anterior end (*fig. 22*). By the activity of these a new branch is formed on each side and the involucre is left behind at the juncture of these two branches.

Lining the walls of the involucre on the inner side, among the archegonia, are large numbers of glandular hairs, which are outgrowths of the superficial cells. These are usually cut off by a transverse wall from the parent cell (*figs. 28, 33*). These slime-secreting hairs

seem, like those of the antheridial cavity, constantly more slender in form than the bent, club-shaped hairs which occur close to the growing point, as was noted by RUGE ('95).

The early stages of the archegonium were not made out as completely as were those of the antheridium, but the stages seen were sufficient to show that the archegonia of Monoclea agree essentially in the early stages of their development with those of other liverworts that have been carefully studied. Thus in *fig. 32* we have a young archegonium with wall cells, a cover cell, and three axial cells of which the lower is evidently destined to form the egg and ventral canal cell, while the upper are to break up into neck canal cells. The structure is in other words identical in all respects with that of the young archegonium of all the well-known Marchantiaceae and Jungermanniaceae (*cf.* CAMPBELL '95, *figs. 2, 17, 46,* and GOEBEL '98, *fig. 137*).

The mature archegonium (*fig. 33*) has a rather broad stalk, a well-marked venter, and, as noted by LEITGEB ('77, p. 67) and RUGE ('93), has also a very long neck (*figs. 28, 29, 33*). In the cavity of the archegonium is found a large, oval egg, a small ventral canal cell, and an unusually large number of neck canal cells. The number of the latter is larger than ten, and in the case figured was apparently fourteen, though the cells shown in dotted outline could not be made out clearly, being located just at the level of juncture of the two adjoining sections from which the drawing was made.

The number of cells seen in a transverse section of the neck of the archegonium is usually six, as shown by CAMPBELL ('98), but occasionally five and frequently seven or eight were found (*figs. 35, 34*).

The twisting of the cells of the neck of the archegonium was not nearly so marked in my material as in that studied by LEITGEB ('77) and RUGE ('93).

As noted above, the hood-like involucre begins its development long before the archegonia are mature, hence, as was pointed out by LEITGEB ('77), it cannot be the result of fertilization as GOTTSCHE ('58) believed. The archegonium shown in *fig. 33* was found in the involucre shown in *fig. 28*. Since the archegonium is practically ripe it seems evident that the fertilization of most if not all of the archegonia must take place before the mouth of the involucre is much contracted. The size of many involucres containing embryos points to

the same conclusion. It may still be, however, that the unusually long neck of the archegonium is of advantage in insuring fertilization, as suggested by LEITGEB ('77, p. 65) and RUGE ('93), though the involucre is not so nearly closed at the time of fertilization as they apparently supposed.

The wall of the venter of the archegonium becomes two-layered before fertilization. After fertilization, as the embryo develops, the venter increases greatly in length and in thickness, forming thus a long tubular calyptra which may be twelve or fifteen cells thick near the base (*figs. 31, 39, 41*). This calyptra is ultimately ruptured near the top by the elongation of the seta, in such a manner usually as to leave it more or less two-lipped.

THE SPOROGONIUM.

The actual fertilization of the egg was not observed. At some time after the maturation of the archegonium, the neck shrivels at the tip, the wall of the venter begins to thicken; the egg then increases in size and cell divisions appear in it (*fig. 38*).

Material was not available for the determination of the sequence of the earliest divisions of the embryo, and from the youngest ones seen it could not be discovered whether these were longitudinal or transverse. That longitudinal walls appear very early is evident from *fig. 36*, and the transverse wall near the middle in this figure may be the primary one of the embryo, as is usual with other liverworts. That there is a quadrant formation in the upper part of the embryo is evident from *figs. 41, 42*.

The differentiation of foot and capsule appears early in the development and is indicated by the more rapid enlargement in diameter of the former and by the larger cells of which it is composed (*figs. 31, 38, 39, 40*). The capsule later increases in diameter so as slightly to exceed the foot, and becomes elongated to eight or ten times its diameter (*fig. 31*). The seta is developed from just above the constricted region that first marks the separation of foot and capsule (*figs. 31, 38, 40*). Later on this constriction is obliterated, the foot and seta differ little in diameter (*fig. 31*), and the foot is not as sharply distinguished from the rest of the sporogonium as is shown by GOTT-SCHE ('59, *fig. 17*).

The longitudinal walls which immediately follow the quadrant-walls in the capsule do not appear in very regular order, but there is soon discoverable an inner series of six or eight cells surrounded by an outer layer of about twice as many cells (*figs. 37, 41, 42*). The latter series form the wall of the capsule, while the former give rise to the spores and elaters (*figs. 40, 43, 44, 45*). Apparently no further periclines are formed in these primary wall cells, except at the top of the capsule (*figs. 31, 45, 48*). Thus all but this portion of the wall is a single layer of cells as described by GOTTSCHE ('58). I have seen no authority for the statement by SCHIFFNER ('93) that the wall is two-layered.

These cells of the wall of the capsule, as has been carefully described by GOTTSCHE ('58), have their walls provided with an elaborate series of thickening bands. The cells of the basal part of the wall are elongated to five to ten times their width, while those at the top of the capsule are nearly equal in length and in tangential width, though somewhat irregular in shape. The rupture of the ripe capsule originates at the top and extends down one side to allow the smooth-edged flaps to open out to the spoon-like form figured by HOOKER ('20). The mature capsule is about 1.5^{mm} in diameter and 6–8^{mm} long.

The seta of the nearly ripe capsule is about 1^{mm} long and in the final stretching to elevate the capsule increases to 30–40^{mm}. Before stretching, the sporogonium has a nearly horizontal position in the involucre, but as the seta extends it curves upward and the capsule finally becomes vertical in position.

Just before elongation the component cells of the seta are 30–35μ wide and 12–16μ long. During elongation the width of the cells changes but little, while the length increases often to 0.5^{mm}.

The division of the archesporial cells in the interior of the capsule goes on without evident differentiation until there are about 30 or 40 cells on a diameter of the capsule (*figs. 43, 44*). Soon after this the cells elongate markedly in a direction longitudinal to the capsule (*fig. 45*.) When their length has reached five to ten times their diameter (*fig. 46*), some of the thicker cells divide transversely and each gives rise to eight cubical spore mother-cells. Other more slender cells continue to elongate greatly to form the elaters (*fig. 47*). The elater-

forming cells are thus not sister cells of the spore mother-cells, but rather of cells which give rise to several of the latter. The longitudinal grouping of the spore mother-cells in *figs. 47* and *49* indicates their origin, and the pointed, terminal mother-cell of each row in *fig. 47* recalls the spindle-like form of the parent cell.

When the capsule is about three quarters grown, that is when it is 3 or 4^{mm} long, the spore mother-cells round off from one another. Soon afterward they assume the usual four-lobed form (*fig.49*). Then follows the division of the nucleus and the separation of the spores of the tetrad in the usual manner. The mature spores are uninucleate, nearly globular, 16 to 18μ in diameter, and have a thick, reticulated wall (*figs. 51, 52*).

The elaters continue to elongate as the spores are maturing and ultimately reach a length of 150μ. They are about 8μ in diameter in the middle, and taper to a rather blunt end in each direction. Some time after the individual spores are formed two rather closely twisted, spiral, thickening bands appear in each of the elaters (*fig. 50*). These bands are about as wide as the interspaces of thinner wall left between them. One of the bands often disappears considerably before the other as the end of the elater is approached. No grouping of the elaters or attachment to the wall of the capsule was noticed, except the attachment of a few scattered elaters at the base of the capsule to the wall near the end of the seta.

The elongation of the seta occurs after the capsule is practically ripe, and the latter opens soon after being pushed out of the involucre. The opening seems to proceed gradually, and the escape of the spores, aided by the twisting and untwisting of the elaters, is thus distributed over a considerable portion of time.

CONCLUSIONS.

HOOKER ('20), GOTTSCHE ('58), and LEITGEB ('77, p. 62, and '81, p. 132) all recognized the similarity of Monoclea in size and habit to the Marchantiaceae, and LEITGEB noticed the likeness in the structure of the antheridium and the male receptacle to those of the same group of liverworts. But the form of the involucre, the structure of the archegonium, and especially the absence of air chambers and (as they believed) of tuberculate rhizoids, led all these workers to keep Monoclea out of the Marchantiaceae.

GOEBEL ('98, p. 240) points out the similarity in the development of the antheridium of Monoclea to that of the Marchantiaceae, which was figured (but apparently not recognized) by RUGE ('93), but still GOEBEL does not definitely include Monoclea in that family.

CAMPBELL ('98) for the first time placed Monoclea definitely in the Marchantiaceae, because of the form of the thallus and the presence of two types of rhizoids, but especially because of the structure of the male receptacle and of the antheridium and archegonium.

Practically all the evidence collected in the present research seems to the writer to favor the view of CAMPBELL. For it is found that the thallus of Monoclea is like that of the Marchantiaceae in gross structure, in the mode of growth and branching, in the type of initial cell, and as I have been able to show in the possession of tuberculate rhizoids as well as thin-walled ones, in which latter character Monoclea differs from all described Jungermanniaceae.

These tuberculate rhizoids have been overlooked by earlier observers probably because of their comparative rarity, and because of the very few tubercles present in each rhizoid (*figs. 23, 24*). The tuberculate rhizoids are 10 to 15μ in diameter, while the other rhizoids are 25 to 35μ in diameter and much thinner walled. The distribution of these two types of rhizoids is perfectly constant, as was shown by LEITGEB ('77, p. 63). The thick-walled ones are scattered more generally over the thallus, and always lie nearly parallel to it, while the thin-walled ones are clearly grouped near the mid-line of the thallus and stand out perpendicularly to it (*figs. 8, 9, 28*). This is just the relative position of these two types of rhizoids in, for example, Marchantia or Fegatella (CAVERS '04, *fig. 17*), where the tuberculate rhizoids arise under the ventral scales along the whole costa and run backward between these scales to the base of the thallus, while the large, thin-walled ones arise in groups and stand straight out from the thallus.

The tuberculate rhizoids of Monoclea are always thin-walled near the distal end, which probably means that there is a long-continued growth in length in this region. Some of them surely reach a very great length.

The absence of the ventral scales characteristic of the other Marchantiaceae, and of the air chambers with their chlorophyll-bearing cells, is probably, as CAMPBELL has suggested, to be regarded

as a reduction due to the nature of the habitat of Monoclea. For, though these plants are not actually submerged, they do live in very wet places and are surrounded by a constantly saturated atmosphere. COKER ('03) has shown that we have an actual example of this sort of reduction in *Dumortiera hirsuta*, plants of which growing in a damp atmosphere on a porous, sandy soil, had well-developed air chambers, while other plants which were constantly wet with dripping water had no trace of such chambers. Even in Marchantia I find that, as was shown by RUGE ('93), submerged plants have imperfect air chambers or none at all. There seems also to be a marked reduction in the size of the ventral scales, in the number of tuberculate rhizoids, and likewise in the number of tubercles in them in these submerged plants.

The facts of vegetative structure referred to strongly indicate a relationship with the Marchantiaceae, and the structure and development of the reproductive organs seem to me to confirm this beyond reasonable doubt.

The male receptacle of Monoclea does not, it is true, closely resemble that of Fegatella, with which it has been most frequently compared, since it has but one growing point, while that of Fegatella has several, as has been shown by LEITGEB ('81, p. 95) and CAVERS ('04). In this respect Monoclea resembles much more certain other genera of the Marchantiaceae. In Corsinia, for example, according to BISCHOFF ('35, pl. 70) and LEITGEB ('79, p. 48), the antheridia arise acropetally on an elongated, thickened, and bordered receptacle very like that of Monoclea in origin and structure. Similar also are the less known male receptacles of Funicularia, according to MONTAGNE ('56), and of Sauteria, according to BISCHOFF ('35) and LEITGEB ('81). Among the higher Marchantiaceae also male receptacles similar to that of Monoclea are not wanting. Thus Aytonia (LEITGEB '81, GOEBEL '98), Reboulia (BISCHOFF '35, LEITGEB '81), Grimaldia (BISCHOFF '35, LEITGEB '81), and especially Fimbriaria (BISCHOFF '35, CAMPBELL '95) show a striking resemblance to Monoclea in the structure and development of the male receptacle. On the other hand there is no structure closely comparable with the male receptacle of Monoclea known among the Jungermanniaceae.

The development and structure of the sunken antheridia of Mono-

clea is still more clearly marchantiaceous in type. The large number of primary transverse divisions in the young antheridium, the mode of separation of the primary spermatogenous cells from the wall cells, and the elongated pointed form of the mature antheridium are, I believe, not found in any of the Jungermanniaceae.

The development of the archegonia directly upon the dorsiventral vegetative part of the thallus has, as was noted above, always been considered a most important difference between Monoclea and the Marchantiaceae, most workers having on this account compared it rather with the genera Pellia and Symphyogyna of the Jungermanniaceae. But even in this feature Monoclea is not without counterparts among the Marchantiaceae. For example, in Funicularia, according to LEITGEB ('79, p. 59) the archegonia are formed in groups of three or four, each group being sunken in a pit in the dorsal side of the thallus and protected by a hood-like involucre, which grows out over the archegonia from behind. Likewise in Corsinia, according to the same author ('79, p. 55), the archegonia arise acropetally in groups of eight or ten exactly as in Monoclea, and are also covered by a similar hood, which however seems to develop after fertilization. This hood may cover all the fertilized archegonia in one pit or there may be several hoods in the same pit, each covering one or more archegonia. In both genera of the Targionioideae (Targionia and Cyathodium) the archegonia arise directly behind the growing point of an ordinary branch of the thallus (LEITGEB '81, pp. 133 and 139, and CAMPBELL '95, p. 54). The two-lobed outgrowth of the thallus found here resembles in origin the involucre of Monoclea, though it remains quite small until after fertilization.

It seems more probable that in the case of Corsinia the wall of the pit as a whole is homologous with the involucre of Monoclea, rather than that each of the hoods is, but the most important character which Monoclea has in common with Corsinia, as well as with the other genera mentioned, is the development of the archegonia on an unspecialized portion of the thallus.

Of the archegonium of Monoclea I have already said that its development and mature structure are typically marchantiaceous. In the very long neck and especially in the six rows of neck cells it differs from all known Jungermanniaceae.

Probably the most serious obstacle of all to putting Monoclea in the Marchantiaceae has been the sporogonium, which with its long seta and its erect cylindrical capsule has quite the aspect of that of certain of the frondose Jungermanniaceae. But even here distinctive marchantiaceous characters are not entirely wanting. Thus, for example, the wall of the capsule of Monoclea is a single layer of cells (*figs. 31, 43*), except near the base and a small area at the top. In this respect it agrees with all known Marchantiaceae (SCHIFFNER '93), and differs from all the Jungermanniaceae with which it has been supposed to be related. For the wall of the capsule of Pellia is well known to be three or four-layered, and I have found that of Symphyogyna to have a similar structure, instead of a one-layered wall as is stated by SCHIFFNER. The slightly developed foot of Monoclea has many counterparts among both Marchantiaceae and Jungermanniaceae. The seta is probably longer than is found in any other marchantiaceous form, but this and the simple type of rupture of the capsule, which occurs in isolated cases in both the Jungermanniaceae and Anthocerotaceae, are perhaps related in some way to the peculiar habitat of the plant. The spores and elaters show, so far as I have discovered, no characteristic peculiarities.

The particular genus of the Marchantiaceae to which Monoclea is most closely related I am at present unable to suggest. We have seen that it resembles certain of the simpler genera in the place of origin of its antheridia and archegonia. These facts seem to me to favor CAMPBELL's view ('98) that the relationship of Monoclea is with the lower Marchantiaceae. The occurrence of similar male receptacles in some of the higher forms, *e. g.*, Fimbriaria and Grimaldia, is probably an instance of the persistence of the primitive type of male receptacle side by side with a more highly specialized female one.

SUMMARY.

Monoclea occurs in Jamaica in very damp places, being usually constantly wet with dripping water.

The male receptacle of Monoclea is only superfically like that of Fegatella, since all the antheridia of a receptacle are formed in acropetal succession from one growing point. It resembles rather that of Corsinia and Fimbriaria.

The antheridium rudiment is elongated, and it divides transversely into six or seven primary cells. The wall cells and spermatogenous cells are separated from each other in the body of the antheridium after the formation of quadrant and octant walls. The mature antheridium is elongated and pointed and is sunken in the receptacle.

In the nucleus of the spermatozoid the individual chromosomes are recognizable as distinct twisted fibers.

The archegonium is very long-necked, has six rows of neck cells and twelve or more neck canal cells. It is probably fertilized before the hood-like involucre has grown far beyond its tip.

The capsular portion of the sporogonium divides to quadrants and octants before sporogenous cells and wall cells are separated. The foot is small, the seta stretches to 30 or 40^{mm} in length, and the extended capsule is erect, elongated, cylindrical, and its wall is a single layer of cells.

Monoclea possesses two kinds of rhizoids, corresponding to those of Marchantia in size, direction of growth, and in the presence of tubercles in those of one type.

The absence of air chambers and ventral scales is probably due to the nearly aquatic habit of the plant.

The evidence gained from the study of the origin and structure of the male receptacle, and of the antheridium and archegonium, and from the structure of the wall of the capsule, and the presence and direction of growth of the two types of rhizoids, favors the view that Monoclea is most closely related to the lower Marchantiaceae.

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EXPLANATION OF PLATES XVI AND XVII.

PLATE XVI.

FIG. 1. View of upper surface of part of a male thallus, showing branching
and three generations of male receptacles. ×1.5.

FIG. 2. Transverse section of a male plant through a mature receptacle.
×5.

FIG. 3. Longitudinal section of male plant through receptacles of two gen-
erations. ×3.

FIG. 4. Diagrammatic view of upper surface of a half-grown male receptacle
with a single growing point; the dotted outlines indicate the location of the anthe-
ridia. × 25.

FIG. 5. Similar view of a male receptacle with two growing points. × 25.

FIG. 6. Upper anterior part of a longitudinal section of a young male recep-
tacle, showing very young antheridia. × 350.

FIG. 7. Longitudinal section of a young male receptacle, passing just at one
side of the growing point; the dotted lines indicate the position of the growing
point in an adjoining section. × 38.

FIG. 8*a*. Surface view of nearly mature spermatozoid, showing the inter-
twisted chromatin fibers. × 1500.

FIG. 8*b*. Diagram of an optical section of such a spermatozoid, showing the
relation of chromatin fibers still more clearly. × 4000.

FIG. 9. Median longitudinal section of an older male receptacle; the letters
indicate the order of origin of the antheridia. × 30.

FIG. 10. Young antheridium and surrounding cells from a section similar
to last. × 350.

FIG. 11. Longitudinal section of a young antheridium, showing the seven primary tiers of cells and the separation of the wall cells from the spermatogenous cells. × 350.

FIG. 12. Similar section of a slightly older antheridium. × 350.

FIG. 13. Similar section of an antheridium and an antheridial cavity of the male receptacle. × 350.

FIG. 14. Longitudinal section of an older antheridium. × 160.

FIG. 15. Transverse section of a young antheridium and surrounding cells showing a primary longitudinal wall of the antheridium. × 650.

FIG. 16. Similar section of an antheridium showing quadrant walls. × 650.

FIG. 17. Similar section of an antheridium in which spermatogenous cells and the antheridial wall have been differentiated. × 650.

FIG. 18. Transverse section of an older antheridium, showing the mode of division of the four primary spermatogenous cells. × 350.

FIGS. 19–20. Similar sections of still older antheridia, showing multiplication of spermatogenous cells. × 160.

FIG. 21. Portion of longitudinal section of nearly mature antheridium, showing the wall and the three-cornered spermatozoid mother-cells. × 350.

FIG. 22. View of the upper surface of part of a female plant, showing an involucre containing two young sporogonia, one containing a nearly full-grown sporogonium, and one from which a capsule has already been extended. × 1.5.

FIGS. 23–24. Optical longitudinal sections of tuberculate rhizoids. × 650.

FIG. 25. Portion of the edge of the thallus with thick-walled marginal rhizoids. × 160.

FIG. 26. Longitudinal section through the growing point of a female plant, showing the beginning of the pit in which the archegonia arise. × 75.

PLATE XVII.

FIG. 27. Lower portion of the same section, showing the slime-secreting hairs and the cells which are to form archegonia. ×350.

FIG. 28. Longitudinal section of an older archegonial pit, showing the half-grown involucre and two mature archegonia. ×38.

FIG. 29. Similar section of a full-grown involucre, containing an archegonium with a young embryo. ×8.

FIG. 30. Transverse section of fertile branch of female thallus passing through an involucre containing a nearly mature sporogonium. ×8.
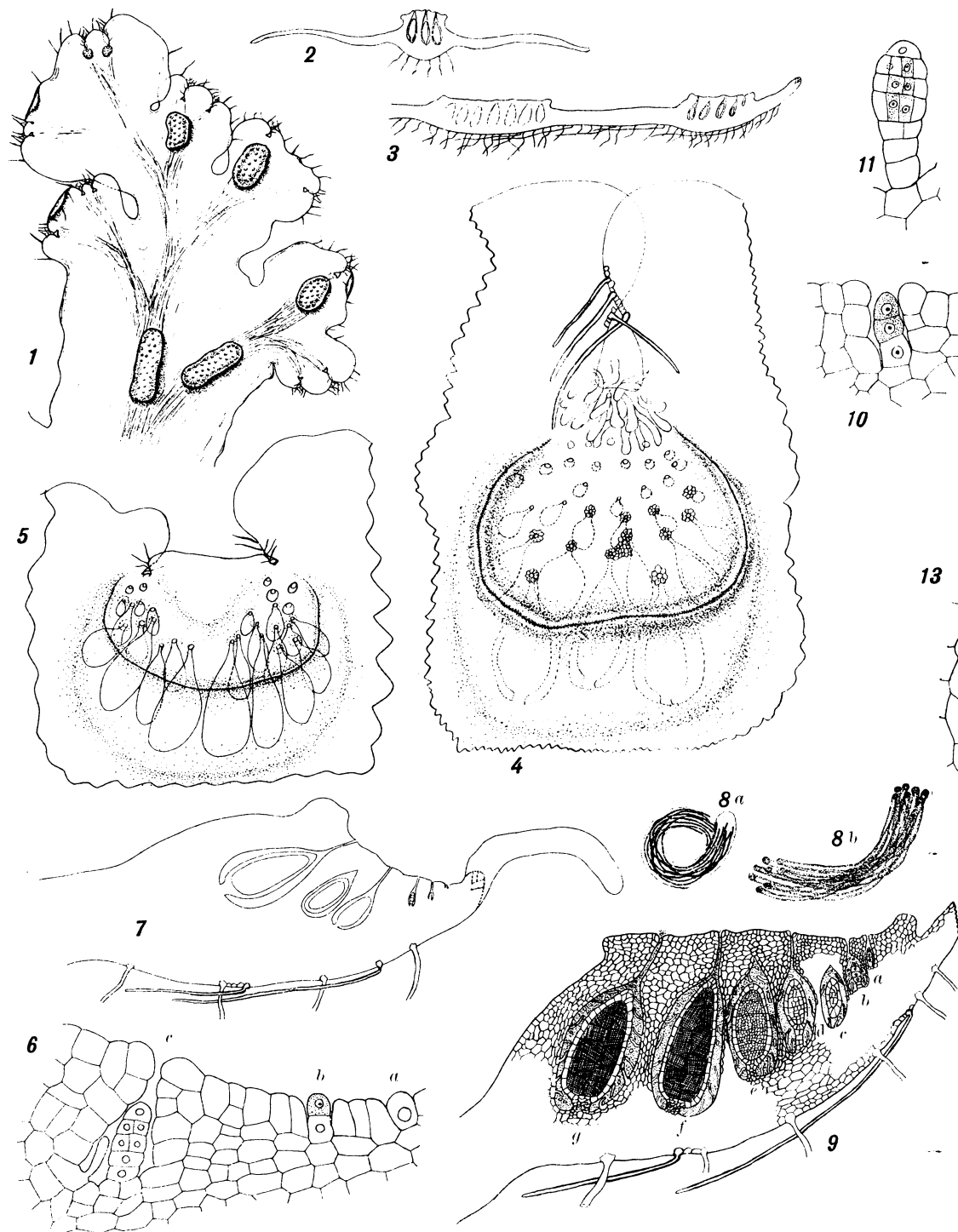
FIG. 31. Longitudinal section of similar involucre and sporogonium. ×8.
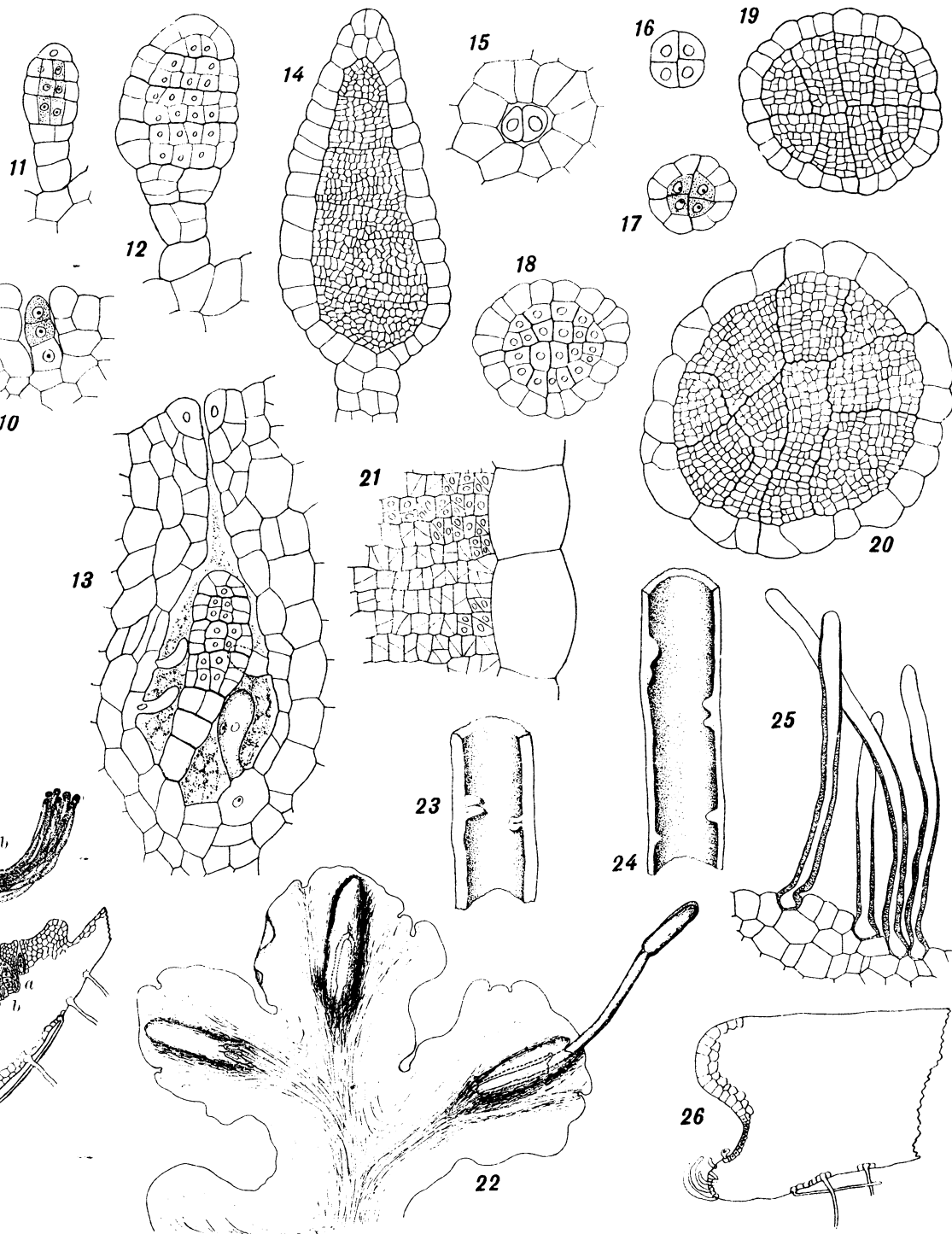
FIG. 32. Longitudinal section of a young archegonium. ×350.
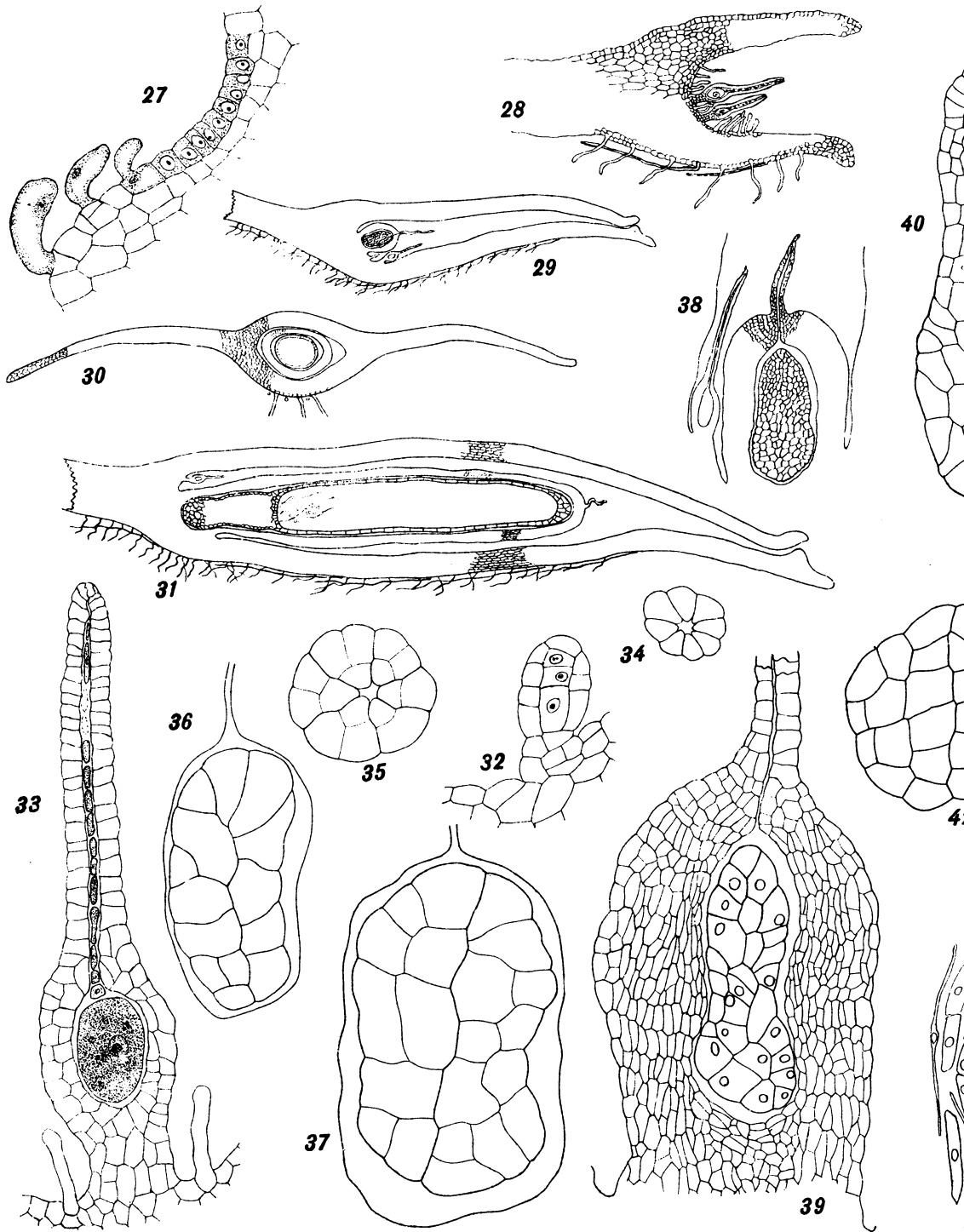
FIG. 33. Longitudinal section of a mature archegonium. ×160.

FIG. 34. Transverse section of neck of archegonium, showing eight neck cells. ×160.

FIG. 35. Similar section of archegonium at juncture of neck and venter, showing a normal six-celled neck. ×300.

FIGS. 36–37. Longitudinal sections of young embryos, showing the earlier walls in the latter. ×350.

PLATE XVI

11 12 14 15 16 17 19 18 20 10 13 21 23 24 25 26 22

PLATE XVII

40

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45

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43

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48

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46

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51

52
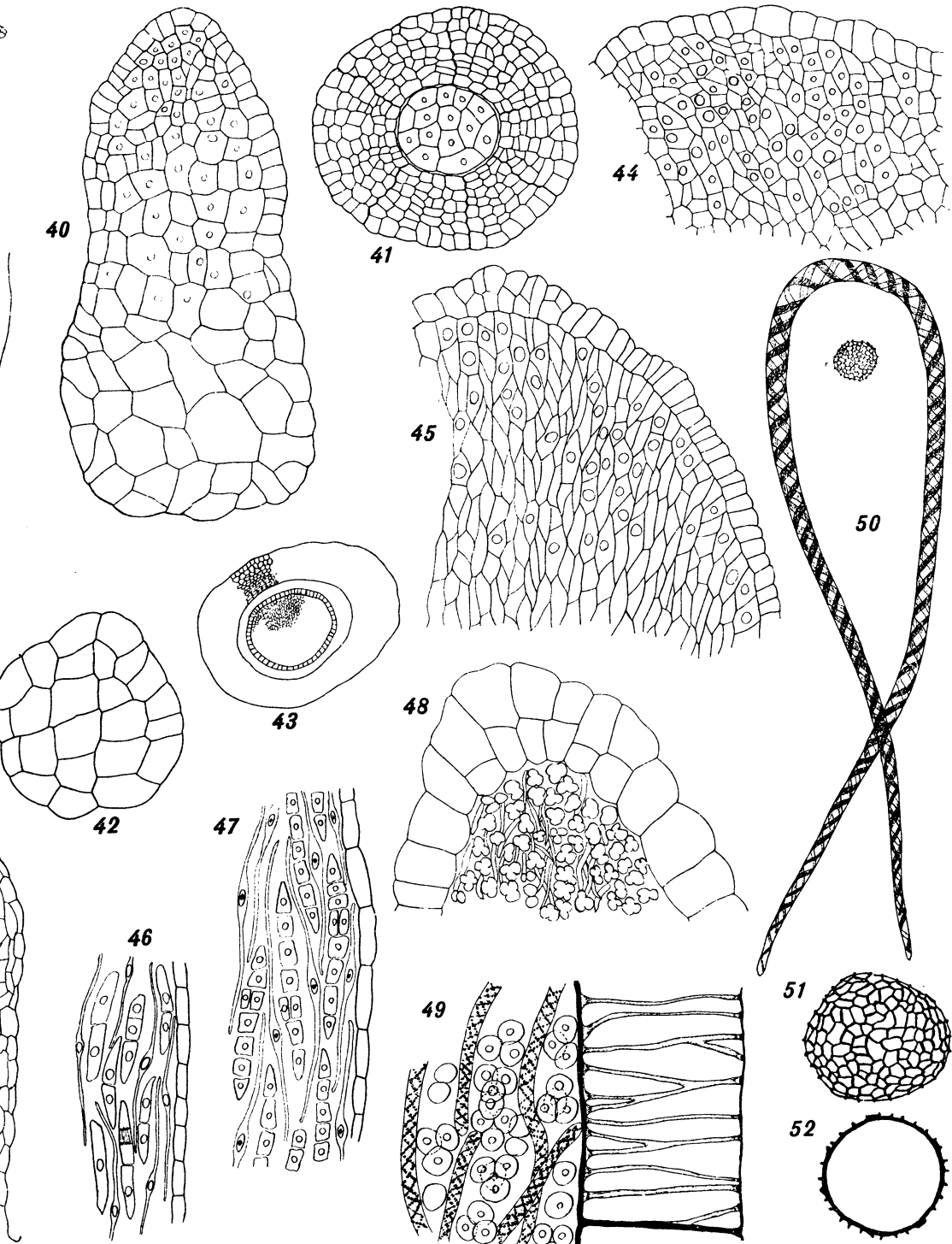
FIG. 38. Longitudinal section of young embryo and archegonium. ×38.

FIG. 39. Similar section with a slightly younger embryo, showing the differentiation of the latter into foot, seta, and capsule. ×160.

FIG. 40. Longitudinal section of an older embryo, showing differentiation of capsule into wall and sporogenous cells. ×160.

FIG. 41. Transverse section of an archegonium and embryo of the age of that shown in *fig. 37*, showing arrangement of cells in the capsular region. ×160.

FIG. 42. Similar section of another embryo. ×160.

FIG. 43. Transverse section of an archegonium, with an embryo showing wall of capsule and isodiametric sporogenous cells. ×38.

FIG. 44. Detail of last. ×350.

FIG. 45. Part of longitudinal section of a capsule of the same age as the last. ×350.

FIG. 46. Part of a similar section of an older capsule, showing elaters and their spindle-shaped sister cells dividing to spore mother-cells. ×350.

FIG. 47. Similar figure from an older capsule, showing elaters and rows of spore mother-cells. ×350.

FIG. 48. Longitudinal section of the tip of a nearly mature capsule, showing two-layered region of the wall and three-lobed spore mother-cells. ×160.

FIG. 49. Elaters, tetrads of spores and a cell, from the wall of a still more mature capsule. ×350.

FIG. 50. Single elater from a ripe capsule. ×700.

FIG. 51. A single spore showing structure of spore wall. ×1250.

FIG. 52. Optical section of spore wall. ×1250.